

The Origin of the Afroalpine Pachycaul Flora and its Implications

by

D. J. MABBERLEY
Botany School, Oxford

Summary

The morphological, anatomical and biogeographical implications of the apparently primitive nature of the forest pachycaul form in *Senecio* and *Lobelia* are discussed. The preadaptation of high altitude swamp pachycaul forms for temperate rhizomatous vegetation and the adaptations of hyperpachycaul forms to the conditions of the tropical alpine belt are stressed.



Fig. 1. *Lobelia rhynchopetalum* in the High Simien of Ethiopia during von Rüppell's expedition of 1833. (From von Rüppell, 1840: t. 6). Reproduced by kind permission of the University Librarian, Cambridge.

"Ausserdem charakterisiert diese Zone eine sehr fremdartige Pflanze, die einer Aloekrone gleicht, welche auf einem mannshohen hohlen Stengel aufsitzt. Ihr Landesname ist Gibarra, und ihr systematische Stelle die Familie der Lobeliaceen. Da sie nur an der Schneeegränze vorkommt, und doch in der Form einige Ähnlichkeit mit den der wärmsten Tropenvegetation eigenthümlichen Pflanzen hat, so gibt dieses der Landschaft einem höchst fremdartigen Charakter."

Eduard von Rüppell (1836).

Introduction

With the baobab and *Welwitschia*, the Giant Groundsels and Lobelias are perhaps the most famous botanical curiosities of Africa. The layman's familiarity with herbaceous senecios and lobelias, the unfamiliar habit of the 'giant' plants and their exotic tropical montane home have given the Giant Groundsels and Lobelias an exalted place in botanical travelogues, popular horticultural works and other writings and made them a tourist attraction attained by few members of the vegetable kingdom.

The adjective 'giant' in botanical works has connotations of teratology or polyploidy and is used here only in the nicknames 'Giant Groundsels' for *Senecio* L. subg. *Dendrosenecio* Hedb. and 'Giant Lobelias' for *Lobelia* L. sect. *Rhyncho-petalum* (Fres.) Benth. & Hook.f., the general term 'pachycaul' being used for those plants with massive primary construction, large buds and large leaves, of which fine examples are provided by the Giant Groundsels and Lobelias (Corner, 1949).

Pachycaul senecios have been known from Africa since the eighteenth century; those first brought back to Britain were not from the continent but from the isolated Atlantic island of St. Helena, 900 km east of the Mid-Atlantic Ridge (Mabberley, 1975b). Later, pachycaul species were discovered in West Africa and Ethiopia where the first pachycaul lobelia was collected (Fig. 1); finally the mountains of tropical East and Central Africa were rediscovered and the famous Giant Groundsels and more Giant Lobelias collected for the first time, in the latter half of the last century.

Meanwhile the alpine belts of the Andes yielded the pachycaul "Frailejones" (*Espeletia* spp.) and puyas, and although pachycaul plants are not restricted to islands and mountain-tops (Corner, 1949), their conspicuous appearance in such situations, and the superficial correlation between their presence and the 'insular situation' had aroused considerable discussion. The study of the floras and faunas of islands, continental and oceanic, and of insular situations, geological and altitudinal, has been of continuous interest to biologists, for much evidence for the theory of Natural Selection was derived from it by Darwin, whose observations in the Galapagos Islands paved the way to modern ideas on evolution:

"The principle which determines the general character of the fauna and flora of oceanic islands, namely that of the inhabitants, when not identically the same, yet are plainly related to the inhabitants of that region whence colonists could mostly readily have been derived — is of the widest application throughout nature For alpine species, excepting in so far as the same forms, chiefly of plants, have spread widely throughout the world during the glacial epoch, are related to those of the surrounding lowlands."

Charles Darwin, *Origin of Species* (1859: 342)

The fallacy in the blind comparison of 'altitudinal islands' and oceanic islands has been explored by White (1971). Nevertheless, certain families, e.g. Campanulaceae and Compositae are represented by pachycaul forms on islands both geographical and altitudinal. One genus in each of these families viz. *Lobelia* and *Senecio* is similarly distributed. Within their respective families, these genera are large, *Lobelia* with perhaps 350 species (Wimmer, 1956, 1968) and *Senecio*, as understood at present, is perhaps the largest of flowering plant genera with 2000-3000 species (Willis, 1973). Unlike other genera with arborescent forms in these predominantly herbaceous families, *Lobelia* and *Senecio* have herbaceous as well as woody forms (Good, 1974: 85) and almost the whole gamut of life-forms represented in their families is to be found in them. If the genera, or sections of them, are monophyletic, then it should be possible to discern evolutionary trends within them and hence investigate the relationship of the pachycaul habit to that

of the herbaceous habit. It is only in the mountains and on the islands of Africa that pachycaul species of both genera grow together. Thus it was felt that a study of these 'Giant Lobelias and Groundsels' would throw considerable light on the evolution of the woody pachycaul in florally advanced families. Currently seven pachycaul species of *Senecio* (Mabberley, 1973a; 1974a; 1975b) and seventeen pachycaul species of *Lobelia* (Mabberley, 1974c) are recognized. Revisions had been made piecemeal before those, but the origin of the pachycaul habit was undecided through the lack of either developmental studies or the comparison of pachycaul with herbaceous forms. In consequence, two opposing theories had been proposed. Fries & Fries (1922) suggested that the pachycauls were primitively forest plants of the Tropics, whereas Cotton (1944) argued that they had arisen from temperate plants which had reached the Tropics along mountain chains and elaborated pachycaul construction there. Recently these arguments have been voiced by Coe (1967) and Carlquist (1965: 199) respectively.

Besides in these speculations, the Giant Groundsels and Lobelias appeared in a more profound work, the Durian Theory of Corner (1949-54b; 1964), the pachycaul construction which they exhibit being a keystone of much of the theory, which argues the origin of leptocaul trees from pachycaul ancestors. Are they relics of those from which the leptocaul and herbaceous evolved and multiplied to populate the temperate zones, or are they rare elaborations of herbaceous groups selected for their longevity in 'insular situations'?

Senecio

The first African pachycaul senecios to be discovered were *S. leucadendron* (Forst.f.) Hemsl. and *S. redivivus* Mabberley, the He- and She- Cabbage Trees respectively, first collected by Banks on St. Helena on Cook's *Endeavour* voyage in 1771 (Mabberley, 1975b). No pachycaul species from the mainland was collected until 1859, when Sir John Kirk collected scraps of a woody *Senecio* on Livingstone's Zambezi Expedition; his specimens were not received at Kew until 1867, by which time the tree had been discovered on Clarence Peak, Fernando Po in April 1860 by Gustav Mann, whose name it bears, *Senecio mannii* Hook.f. It is now known from Nigeria, Cameroun and from Zaïre to Ethiopia and Tanzania, Mozambique and Angola (Mabberley, 1973b). In June 1864, the Middle East botanist Wilhelm Georg Schimper collected a related species, *S. gigas* Vatke, on his third expedition in Ethiopia.

It was not until the Royal Society and the British Association put the 'Kilimanjaro Expedition' of 1884 into the field with the energetic Harry Hamilton Johnston as its leader that the first Giant Groundsel was collected and named *S. johnstonii* Oliv.; later many collections from the other mountains were also given specific rank, but with *S. johnstonii* these are now considered to constitute three species in all (Mabberley, 1973a), the second being *S. keniodendron* R.E. & T.C.E. Fr., an hyperpachycaul tree of Mt. Kenya and *S. brassica* R.E. & T.C.E. Fr., a 'creeping tree' of Mt. Kenya and the Aberdare Mts. of Kenya. The African pachycaul senecios are thus: *Senecio leucadendron*, *S. redivivus*, *S. mannii*, *S. gigas*, *S. johnstonii* comprising eight geographical and altitudinal subspecies including subsp. *refractisquamatus* (De Wild.) Mabberley and subsp. *barbatipes* (Hedb.) Mabberley, *S. keniodendron* and *S. brassica*.

In Hoffmann's treatment of *Senecio* (1892), all the Giant Groundsels then known as well as the Cabbage Trees and *S. mannii* and *S. gigas* were included in the 'Arborei', an heterogeneous assemblage of species put together merely on their woody habit; some leptocaul shrubs of Madagascar were also included. Recent

study of the details of the flowers (Mabberley, 1974a) has shown that the allegiance of the Giant Groundsels is with the herbaceous sect. *Crociserides*, that of *S. gigas* and *S. mannii* with the lianoid and herbaceous '*Crassocephalum-Gynura*' complex, whilst *S. leucadendron* is quite isolated in the genus as is *S. redivivus*. It is more easily argued (Mabberley, 1974a) that the tropical pachycauls with the primitive '*Dendrosenecio*-branching' are relics of a pachycaul ancestry for the herbaceous group than that they are sporadic arborescent innovations from primarily herbaceous stocks. This is supported by the observation that pachycaul trees with this branching habit are to be found in other alliances in *Senecio* in New Zealand, Mexico, Cuba and the Canary Islands.

It was argued that in the *Dendrosenecio-Crociserides* assemblage, evolutionary trends within the Giant Groundsels provided a clue to the origin of the herbaceous forms by the stem's becoming a '*truncus superficialis*' as in *S. brassica* and thence a subterranean rhizome suited to perennation and the invasion of the temperate zones (c.f. 'herb-making' in *Hedysarum*, etc. analyzed by Gatsuk, Dervis-Sokolova, Ivanova & Shafranova (1974)). The massive alpine pachycauls, 'hyperpachycauls', are seen as dead ends as far as evolution of temperate vegetation is concerned, but adapted to the exacting climate of the afroalpine belt in elaborating characters such as leaf-movements etc. (see below). By contrast the creeping form adapted to the swampy habitat is seen as pre-adapted to a seasonal climate.

ALPINE PACHYCAULS

In the pachycaul alpine species are elaborated certain characteristics which are weakly developed in the forest forms. Marcescence is more marked; Hedberg (1964) has shown that the marcescent collars of leaves act as efficient insulators, the temperature around one tree dropping to -4°C , whilst remaining $+1.8^{\circ}\text{C}$ within the 'collar'. This warm microhabitat is exploited by animals, e.g. the frills of *S. keniodendron* provide a night shelter for the chironomid midges which breed in the buds of Giant Lobelias, and for many beetles and spiders (Coe, 1967) whilst the groove-toothed rat, *Otomys orestes orestes* Thomas burrows up into the marcescent leaves and leaf-bases (Coe, 1967). In another tree, Hedberg (1964) found that the pith remained at $+3^{\circ}\text{C}$ whilst the temperature dropped to -5°C outside. If the collars are removed, Hedberg suggests that the tree may die. In *S. johnstonii* subsp. *barbatipes*, an alpine plant of Mt Elgon, the rôle of the frills is taken by the highly developed bark, which is again exploited by animals. As *Dendrosenecios* are hygrophilous, they are often to be found in hollows which are frost pockets, where insulation is even more important than in the plants of the steep slopes. The movements of the leaves which protect the bud (Diels, 1934: 68) and the production of antifreeze slime are also exploited by the invertebrate fauna which overnight in the ameliorated micro-habitat thus provided, e.g. snails and insects which also receive shelter from desiccation by day (Coe, 1967).

The marked xeromorphy of alpine forms (Hare, 1941) is linked with the severe alpine climate; the thick leaves may be important in preventing water loss. The pubescence of the leaves of many forms may reflect incoming radiation (Hedberg, 1964), but several alpine forms, e.g. *S. keniodendron* have glabrous leaves. The shiny adaxial surface may be of importance in reflection of radiation. The *abaxial* surface of the leaves of *S. brassica* may protect the bud at night when closed over it by preventing outward radiation, as has been discovered by the scarlet-tufted malachite sunbird, *Nectarinia johnstonii johnstonii* Shelley, which gathers the hairs to line its nest (Coe, 1967). There is marked endemism in the insects paralleled by their host distribution patterns. Further, there is an increase in flightlessness with altitude, probably associated with the alpine habitat favouring 'cryptozoic' modes of life (Salt, 1954).

Lobelia

The first pachycaul *Lobelia* from Africa was collected by the zoologist, Eduard von Rüppell, in the High Simien in Ethiopia in 1833 (Fig. 1). Now seventeen (one undescribed) such species are known and all are referable to sect. *Rhynchoptalum* (Fres.) Benth. & Hook.f. (Mabberley, 1974c), in subsect. *Haynaldianae* E. Wimmer, subsect. *Nicotianifoliae* Mabberley and subsect. *Rueppellianae* Mabberley. The *Haynaldianae* are a Brazilian group with three African outliers. The *Nicotianifoliae* are found from eastern Africa to S.E. Asia with closely related taxa in Hawaii (Mabberley, 1974c). They include *L. giberroa* Hemsl. of montane forest and clearings and *L. bambuseti* R.E. & T.C.E. Fr. of the upper forest belt. The alpine species are the creeping *L. deckenii* (Asch.) Hemsl. and *L. rhynchoptalum* Hemsl. of the *Rueppellianae* and, of the *Nicotianifoliae*, *L. wollastonii* Bak.f. and *L. telekii* Schweinf., which seem to be parallel alpine types as is *L. nubigena* Anth. of Bhutan in the *L. nicotianifolia* [Roth ex] R. & S. complex. All seem to be derived from forest ancestors (Mabberley 1974c, 1975a). In the Far East the *Nicotianifoliae* include the rhizomatous *L. sumatrana* Merr. of high mountains.

ALPINE PACHYCAULS

The stems of the forest species of Giant Lobelia are usually bare of marcescent foliage; the stems of the alpine species are either prostrate, as in the paludal *L. deckenii*, acaulescent as in *L. telekii*, or erect, with a conspicuous frill of marcescent foliage like that of a *Dendrosenecio* as in *L. wollastonii*. The base of the leaf has a plug of corky tissue which holds the withered lamina to the stem. Erect flowering shoots of *L. deckenii* are also thus clothed as figured by Hedberg (1964). Diurnal leaf movements of the leaves also protect the buds which are bathed in antifreeze slime as in *Senecio*.

Coe (1967) reports that chironomid midges shelter in the closed rosettes of *Lobelia deckenii* subsp. *keniensis* and that the larvae are found in the slimy water therein. The water is said never to dry up, even in cultivation (McDouall, 1927) and does not freeze solid except at very low temperatures: the larvae are thus protected. Hedberg (1964) measured the temperature outside and inside the bud of *Lobelia telekii* and found it to drop to -3.5°C outside, whilst falling no lower than $+1.0^{\circ}\text{C}$ within.

Scott (1935) worked on the assemblages of Coleoptera restricted to the pachycaul lobelias. Some species, e.g. a silphid, spend their entire life cycle in a *Lobelia* plant as do certain bibionid flies in *Lobelia* flowers (Coe, 1967). The distribution of the associated species of *Trechus* (Coleoptera) matches that of the lobelias (Scott, 1958). As with those of the *Dendrosenecios*, many of the insects are flightless and 'giant' within their own genera.

Dendrosenecio, Rhynchoptalum, and Altitudinal Distribution

The study of the pachycaul *Lobelioideae* and *Senecioneae* of Africa has given support to Croizat's (1962: 257) forecast of 'similar' evolutionary patterns in the Giant Groundsels, Lobelias and the South American espeletias. This study has supported the view of the origin of alpine forms from forest ones in parallel as supposed by Humbert (1935) for *Dendrosenecios* and Fries & Fries (1922) for *Lobelia*.

Dendrosenecios occur on the wet mountains of eastern Africa at altitudes over 2100 m, but only on those mountains higher than 3300 m. Although found on the Cheranganis (c. 3400m), they are not found on the nearby Mau Massif (3050m); the difference between these two appears to be critical. Similarly, the difference between the Aberdares (3940m) and the Cheranganis may be critical for *Lobelia telekii*, which is absent from the latter range.

Dendrosenecio and *Lobelia telekii* distributions may be explained by the hypothesis of Wood (1971), wherein former amelioration of climate would have forced the *Senecio* and *Lobelia* belts to higher altitudes; those mountains, which were high enough to harbour them then, still possess them, now that the vegetation belts are once more depressed. The adaptive radiation of the *Dendrosenecios* seems not to have proceeded as far as that in *Lobelia* in the East African mountains. It may be that the longer life-cycle of the *Dendrosenecios* has permitted slower change (c.f. Arber, 1928).

Argument

Starting from the pachycaul members of both genera, interpretations of many morphological and ecological features are possible. Can as much be explained if herbs are taken as the primitive condition and the pachycaul as the advanced?

Starting from herbs in the *Crassocephalum*-*Gynura* and *Crociserides* alliances of *Senecio*, it is necessary to postulate a mechanism for increasing woodiness (that so far suggested (Carlquist (1962)) seems to be untenable (Mabberley (1974b)), and for postponing flowering. All the available evidence points to a forest ancestry for the creeping swamp pachycauls and the erect alpine 'hyperpachycauls' so that there would be no indication of how the presumed herbaceous ancestors attained the forest pachycaul condition. *S. brassica* would be a 'herb' for the second time in its evolution (c.f. Arber, 1928). It would have to be argued that the characteristic '*Dendrosenecio*-branching' ('Modèle de Leeuwenberg' of Hallé & Oldeman, 1970) had been attained in herbaceous, succulent, woody, lianoid and pachycaul groups independently; furthermore, in the wholly pachycaul groups, there would be no indication of their presumed herbaceous ancestors.

Similarly, it must be argued that several herbaceous lines of distinct appearance, e.g. in *Lobelia*, plants like *L. sumatrana* and *L. deckenii*, have colonized the Tropics and produced very similar pachycaul plants in America and Africa as well as India and Hawaii. It must also be assumed that the inflorescence has become more complicated, the fruit baccate, the seeds winged and the leaf-size increased, all in several lines. If this is so, then wind-pollination and dispersal must be antecedent to bird and insect pollination and dispersal, the short-lived temperate herb antecedent to the tropical pachycaul (c.f. Mabberley 1975a).

No sense can be made of phytogeography, associations with animals or the origin of a range of life form within plant genera. It is simpler, then, to follow the easier line of argument, and, in short, arrive at the same conclusion as Corner (1967b) working with the woody genus *Ficus*, for if the herb (*Senecio*, *Lobelia*) or leptocaul tree (*Ficus*) is primitive and the pachycaul advanced, then:

(i) The primitive species are the most common and widespread, contrary to much of biogeography which would have the primitive as relics;

(ii) the pachycauls are advanced but make least contribution to tropical forest (*Ficus*) or temperate floras (*Senecio*, *Lobelia*) which the flowering plants have been evolving;

(iii) the most leptocaul trees (*Ficus*) or herbs (*Senecio*, *Lobelia*) have the simplest inflorescences, supplying no evidence of their evolution.

As Corner continues, morphological series, [whether in *Ficus*, the *Crociserides*, '*Crassocephalum*' or *Rhynchoptetalum*] can be read in either direction; the ecological factor is 'time's arrow'. In the case of *Ficus*, the arrow is aimed at tropical rainforest *via* leptocaul trees; in the *Crociserides* it is aimed at the conquest of the temperate zones *via* preadapted rhizomatous perennials, in '*Crassocephalum*' at filling the secondary habitats of the African Tropics with fast-growing plants and in *Rhynchoptetalum* it is aimed at both.

The hypothesis

The hypothesis is that *Lobelia* sect. *Rhynchoptalum* and *Senecio* sect. *Crociserides* are derived from pachycaul ancestors and that, in parallel, these groups have given rise to herbs which have reached the temperate zones, and to extreme 'hyperpachycaul' forms which have conquered the tropical mountains of Africa, living in wet situations above the treeline away from other arborescent competition. The hypothesis implies that there have been physiological and morphological adaptations for simplification and overwintering in the herbs and remarkable elaborations of characteristics of the forest plants in the hyperpachycauls adapted to the alpine environment.

The evolution of subg. *Dendrosenecio* and sect. *Rhynchoptalum* in Africa can be seen as the conquest of the highlands, either by becoming hyperpachycaul with marcescent foliage, reduction of hydathodes, enhanced pubescence, etc., or by becoming prostrate and lying down in wet places. The latter is the method which has permitted the colonization of the temperate zones in these groups. The marked increase in pachycauly with altitude may have an ecological explanation, for Daubenmire (1947: 186) has shown that massive organs may withstand short periods of extreme temperatures better than less massive ones. Hyperpachycauls are thus adapted to diurnal climate fluctuations, whereas rhizomatous plants with intermittent growth are adapted to a seasonal climate. It becomes clear then, why no *Lobelia* of North Africa and the Mediterranean is of the *Rhynchoptalum* alliance compared with the *Crociserides* with many Asian and European relatives, for, in Africa, the alpine species which reaches furthest north is the hyperpachycaul *L. rhynchoptalum* with a highly peculiar structure; herbaceous *Rhynchoptala* are the result of 'miniaturisation' (Hallé & Oldeman, 1970: 150) in the Far East.

On the other hand, sect. *Rhynchoptalum* has reached the Pacific as fast-growing pachycauls from both east and west, such that the presence of pachycauls on both sides of the Pacific is readily explicable (Mabberley, 1975a). Indeed, the immigration of the 'pachycaul starter' has permitted the development of herbaceous plants from Japan to Sumatra. By contrast the *Crociserides* seem to have spread very little as pachycauls but have romped and excelled in the temperate zones as coarse herbs.

Sect. *Rhynchoptalum* and '*Crassocephalum*' have elaborated fast-growing pachycauls, which have thus become 'nomads' (van Steenis, 1958) of the sub-montane forests of Africa, and India, incidentally predisposing them to cultivation as *shamba* [small-holding] hedges (*S. mannii*) (Mabberley, 1974a) and as pot plants (*L. nicotianifolia* [Roth ex] R. & S. (Anon., 1904) etc.) in Victorian green-houses. By contrast, subg. *Dendrosenecio* with a longer life-cycle has ascended the mountains to make woodlands above the 'treeline'.

In general, then, there is factual support for the predictions of the Durian Theory, with the important proviso that the groups here studied are capable of hyperpachycauly under the selective pressure of the alpine environment.

Implications

According to our hypothesis, then, such statements as "... highly probable that the development of the arborescent habit and delayed flowering among the tree *Senecios* and *Lobelias* of the East African Mountains, was a photoperiodic response ... fixed by Natural Selection", (Melville, 1953) and "The ancestors of the equatorial alpine rosette trees are temperate zone herbs, which arrived on the equatorial peaks by long distance dispersal just as did the ancestors of island rosette trees" (Carlquist, 1965: 200) seem to be unsubstantiated by the available evidence. On the contrary, it is more easily argued that the pachycaul state is the primitive, which leads to the following considerations.

GROWTH HABIT

Herbs

The primitive growth-form in the *Senecioneae* appears to be *Dendrosenecio* branching, examples of which are found scattered throughout the tribe; it appears that it represents the 'pachycaul starter' condition for 'Senecio'. The aerial parts of the *Crociserides*, so difficult to describe in 'cauline' terms appear to be inflorescences and are more readily comparable with one another and other life-forms once this is recognized. Similarly, the creeping lobelias like *L. sumatrana* show that the aerial parts of many lobelias are also merely 'inflorescence'.

Hyperpachycauly

Enhanced pachycauly exemplified in the alpine hyperpachycauls is a feature of both genera. It appears to be associated with the basally growing leaves in these families. Thus, under the selective forces of the alpine environment, there are hyperpachycaul *Dendrosenecios* and lobelias in Africa, *Pachypodium* in the Malagasy Mts. (Koechlin, 1969), espeletias in the Andes (Smith & Koch, 1935), *Saussurea gossipiphora* D. Don and *Rheum nobile* Hook.f. & Thom. in the Himalaya (Anthony, 1936) and, under the selective forces of the horticulturalist, the hyperpachycaul vegetables such as lettuce and cabbage, large European and Asiatic varieties of which are figured by Herklots (1972: 190–224).

The pachycaul construction of massive buds permits the tolerance of the *Tageszeitenklima* (Troll, 1947) of the tropical alpine belts by 'arborescent' plants above the tree-line, e.g. besides *Senecio* and *Lobelia* in Africa, *Puya ramondii* Harms and *Lupinus weberbaueri* Ulbr. in the Peruvian Andes (Pontecorvo, 1972), *Lupinus alopecuroides* Desr. (Heilborn, 1925), puyas and espeletias in the Colombian Andes (Fosberg, 1944) as well as the Andine *Ceroxylon* (Corner, 1966: 289) and even *Cyathea* in the Papuan mountains (Wardle, 1971), but not their spread beyond the Tropics into a seasonal climate. Such diurnal fluctuations in deserts may favour pachycauly e.g. Cactaceae, succulent *Euphorbia* species, *Yucca* spp. etc., and fire may favour pachycaul forms with wide cortex and hence deeply seated or weakly developed cambium, e.g. *Xanthorrhoea* spp. in Australia, *Aloe capitata* Bak. var. *cipolinicola* H. Perr. in the 'prairies' of Madagascar and again *Cyathea* in New Zealand and New Guinea. In the dicotyledonous examples there is a reduction in branching, and in *Puya*, the inflorescence is unbranched in *P. ramondii*. Similar simplification of structure is to be found in *Echium* (Bramwell, 1972a). In that genus, and other 'temperate' genera, the pachycauls of the Canary Islands appear to represent relics of the pachycaul starters which initiated the herbaceous lines so common in Europe, e.g. *Echium* (Meusel, 1952; Bramwell, 1972a), *Sonchus* (Bramwell, 1972b), *Carlina* (Meusel, 1952). Similarly, species of *Erysimum*, *Crambe*, *Aeonium*, *Chrysanthemum*, *Campanula*, *Bupleurum*, *Dendriopoterium*, *Bencomia*, *Digitalis* and *Limonium* ('Statice') appear as pachycaul relics in the Atlantic Islands (Meusel, 1952).

STEM ANATOMY

In general, the anatomy of the herbs in *Senecio* and *Lobelia* is a good deal simpler than that of their pachycaul relatives — fewer cell-layers, leaf-traces, ducts, less modification in the pith and cortex with aerenchyma etc. The seedlings of the pachycauls are more 'conventional'; the differences arise when the apex increases in size.

Cortical and medullary bundles

Associated with hyperpachycauly, there is the appearance of the phylloclad leaf-base and cortical bundles in *Lobelia*; some species have relic medullary bundles showing that the medullary bundle condition is the primitive one in

Lobelia, and the cortical bundle condition the advanced. Davis (1961) points out that in the Compositae, medullary bundles are particularly abundant in the *Cichorieae*, especially in those plants with the 'rosette-habit'.

In *Lobelia*, the medullary bundles serve the base of the primitive 'forest leaf'; the cortical bundles are often associated with the phyllodic leaf. In a similar way, cortical bundles are often associated with leaves of the 'monocotyledonous' type in the Dicotyledons, e.g. *Eryngium* spp. of the monocotyledonous habit (Metcalf & Chalk, 1950: 717), *Gentianaceae-Gentianoideae* (*ibid.*: 933) and groups with leaves which have few costae, e.g. *Melastomataceae* (*ibid.*: 637).

The appearance of cortical bundles seems to be a 'way out' in evolutionary lines where a larger leaf is being favoured and yet the number of traces to serve such a leaf has been lost; hence in *Lobelia*, the cortical bundles are found in the most massive pachycauls (*Rueppellianae*), whose massiveness has been selected for by the alpine and swamp environments. Such bundles also give support to those massive inflorescences formed by the reduction of branching of a forest form, and for which the capacity for supporting lignification has been lost.

It has recently been suggested (Zimmermann & Tomlinson, 1972) that the regular dicotyledonous ring of vascular bundles may be the equivalent of the outer of the monocotyledonous systems seen in some woody monocotyledons. If this is indeed the case, then *Lobelia* sect. *Rhynchoptalum* may demonstrate how the two systems as exemplified by *L. gibberoa* may give rise to the typical dicotyledonous system as seen in *L. bambuseti* by loss of the inner system and the origin of a 'monocotyledonous' system as shown by *L. rhynchoptalum* with the appearance of a 'new' cortical system associated with basally growing leaves (*c.f.* Burt, 1974).

Hyperpachycauly

Selection has favoured the hyperpachycaul in the extreme alpine climate; the hyperpachycaul is marked by its massive apex and reduced branches compared with its forest relatives. Dominance of the apex over lateral meristems is found in the absence of suckers in *L. wollastonii*, the unbranched inflorescences of the alpine *L. rhynchoptalum*, *L. wollastonii*, etc. with the basipetal inflorescence gradient (Mabberley, 1975a) lost etc., the untoothed leaves of alpine *Nicotianifoliae* and the large capitula on weakly branched inflorescences of the alpine *Dendrosenecios*; in short, there is a common constraint determining the morphology of the hyperpachycaul 'syndrome' (*c.f.* Beketoff, 1858; Uittien, 1928; and the particular case of *Sonchus* (Bramwell, 1972b)). The balance of growth factors determining differentiation in the tissues must be tipped in favour of apical dominance. Such may be an increase in 'auxin' as has been suggested by Cotton (1944) and was discovered in *Aster* by Delisle (1937) who found that there was more auxin in the apices of the inflorescences of *A. novae-angliae* L. than in those of *A. multiflorus* Ait. which is much more branched, (*c.f.* also Smith, 1967).

LEAF

Venation

The venation of *Senecio* (Mabberley, 1973a) and *Lobelia* (Mabberley 1974c) leaves is mainly or entirely basipetally formed. In *Dendrosenecio*, the fraction of the leaf formed acropetally is very small; some herbaceous species have a larger part of the lamina thus formed and may be amphipetal.

In the East African *Lobelias*, my studies have shown a series demonstrating the loss of teeth and acropetally formed venation. This series is interpreted as the failing of the marginal meristem in the leaf with the consequent loss of teeth, and the increasing importance of the spreading growth of the 'midrib', giving the phyllodic leaf-base. The reduction of toothiness in both *Senecio* and *Lobelia* reduces the number of hydathodes per leaf. The action of hydathodes is not well understood;

despite their supposed efficiency in extruding water, the hydathodes of the toothed leaves of *L. assurgens* L., a pachycaul of Jamaica, investigated by Shreve (1914) could not prevent the 'injection' of the leaves by water during heavy rain.

The reduction of the acropetal venation would appear to be irreversible. Vassal (1970) has shown the appearance of the phyllodic leaf in *Acacia* to be polyphyletic and formed in various ways, but that there is a progressive loss of pinnae, with a 'mucro' left in some species, as in *Senecio* and *Lobelia*.

On the other hand, there appears to be a constraint on the number of primary costae derived from basipetal development of the lamina. In *Senecio*, the largest leaves have about 18–20 veins in *Dendrosenecio*; most herbaceous species have costal numbers lower than 18. However, some coarse herbaceous species of Uruguay, e.g. *S. bonariensis* Hook. & Arn., appear to have very large numbers of costae; on close examination, it can be seen that the intercostals have been 'pulled out' during development, thus increasing the apparent costal number, as in *S. keniodendron*, (Mabberley, 1973a).

Abscission

Abscission is not a common characteristic in the Compositae (Bentham, 1873), and is almost restricted to those shrubby and arborescent plants of leptocaul construction with narrow leaf-bases, e.g. *Brachylaena*. These characters tend to be associated with the discrete midrib and looped costae, early-formed venation consummate with compact buds and the sudden expansion of intermittent growth, making them comparable with other tree leaves. The insulating marcescent frills and persistent leaf-bases of *Dendrosenecio* and *Lobelia wollastonii* are conspicuous in the afro-alpine flora. When young, however, all *Dendrosenecios* and *Lobelia* sect. *Rhynchopetalum* display this phenomenon, as do herbaceous species, e.g. *L. urens* L., where the rootstock is covered with persistent leaf-bases (Brightmore, 1968).

How widespread is the absence of abscission and the persistence of leaf-bases? Within *Senecio*, all herbs examined have persistent leaves and it appears very commonly in the herbaceous Compositae but is more familiar to flower arrangers than to monographers. The shrubby *S. hypargyreaus* DC. (Madagascar), the climbing *S. maranguensis* O. Hoffmann (Tanzania) and the leaf-succulent species are exceptions. Their small-based leaves are easily lost, even during drying in the press. In the shrubby Compositae, leaf-fall is often not clear-cut and the marcescent foliage makes a useful character for recognizing sterile Compositae in 'the bush'. The leptocaul *Brachylaena* loses leaves as others are formed (Humbert, 1962: 45) or may lose them altogether in the cold season (Lecomte, 1922). However, marcescence is a general feature of herbs and pachycauls of Compositae, e.g. the pachycaul *Espeletia* in the Andes and pachycaul *Conyza vernonioides* (A. Rich.) Wild of East Africa. Such persistent leaf-bases cover the 'stock' of many herbs, e.g. *Andryala* spp. and *Senecio asperulus* DC. (Hutchinson, 1946: 255), and make the climbing hooks of *Mikaniopsis* (Exell, 1956). Comparable contrast of leptocaul and pachycaul and herb is to be found in the Boraginaceae (*s.l.*) with pachycauls, e.g. *Echium* spp. of the Canary Islands, and herbs, e.g. *Myosotis*, with marked marcescence, compared with the leaf-dropping trees, *Cordia* and *Ehretia*, of the Tropics.

Much has been written of the 'abscission layer' with regard to marcescence, but Gawadi & Avery (1950) pointed out that abscission is not always associated with such a layer and that the layer is a protective feature of the cicatrice; indeed, it sometimes appears after abscission. Nevertheless, the range of forms of marcescence and abscission in monophyletic groups shows that abscission has been gained or lost many times in the angiosperms.

Many young tropical trees retain their leaves in the dry season (Schaffalitzky de Muckadell, 1959) rather like the beech (Knight, 1795) in winter or when kept horticulturally short as a hedge. It is one of a syndrome of 'juvenile' characters (Schaffalitzky de Muckadell, 1959) which appear to represent a primitive condition in wood anatomy etc. (Mabberley, 1974 a-b).

If it is postulated that the primitive pachycaul had marcescent leaves, it seems reasonable to argue that such marcescence may have been selected against with the increasing trunk size due to increasing wood formation through secondary thickening, but elaborated where such a mantle would act as an insulator, e.g. in hot conditions the Joshua Tree (*Yucca brevifolia* Engl.) of the deserts of S.W. United States (Menninger, 1967: 2) and in the cold, *Espeletia* in the Andes. The origin of the leptocaul tree in many lines according to the Durian Theory must have been accompanied by the origin of the small leaf with abscission which seems to have been achieved in various ways (Gawadi & Avery, 1950); especially efficient abscission mechanisms would have been selected for in seasonal conditions, such as 'savanna' and the temperate zones.

EUROPEAN FLORA

The ecological preference of lobelias for wet places (Woodhead, 1951a) is a direct result of a wet tropical ancestry through upland swamp habitats to the temperate zones; the predominance of aerenchyma and hydathodes in *Lobelia* is thus explicable as is the remarkable habit of the aquatic *L. dortmanna* L. The rare branching of *L. dortmanna* inflorescences (Woodhead, 1951b) is explicable as an ancestral trait, and the minute undeveloped flowers at the apex and smaller cell-size in the upper leaves (Tenopir, 1918) are to be expected from the primitive 'die-away growth' (Corner, 1949) of the primitive tropical pachycaul ancestor.

Pachycaul Outlook

We need to know more of pachycaul plants (Corner, 1967a). In the Compositae, we want to know how some tribes have elaborated leptocaul trees as in *Dicoma* and *Brachylaena*; the latter genus has even reached the 'willow pattern stage' (Corner, 1964: 143), the ultimate in leptocauly, in *B. neriifolia* R.Br. (Hutchinson, 1964: 228). Such pachycaul-leptocaul trends are not open to simple computer analysis, for they are in parallel within related phylads. Are the principles governing pachycauly in Compositae and Campanulaceae of general application?

In Compositae, we need to know more of hyperpachycauly and the reappearance of the big leaf when the acropetal venation has been lost, as in the lettuce in cultivation, and why the basipetal venation of Compositae never seems to exceed about eighteen major costal pairs. We need to know more of the pachycaul *Dendrocacalia* of the Bonin Islands (Tuyama, 1936) and of the Siberian *Petasites* the petioles of which are higher than a man (Gilbert-Carter, 1947: 143). We need to know more but we are almost too late: introductions of continental plants to the islands of Hawaii and St. Helena, and the introduction of animals to those islands and to Kerguelen have had disastrous effects on the passive native pachycauls. In the mountains, the puyas are being grubbed up by shepherds, for lambs can get entangled in *Puya* spines (Pontecorvo, 1972) and in Africa, the *Dendrosenecios* of Kilimanjaro are becoming rare through excessive cutting (Hedberg, 1969). Having fled the rising forests of leptocauly to reach the refuge of islands and mountain, the pachycauls are now cornered by Man the Explorer and Exploiter. We scarcely have time to begin to follow the leads to an understanding of plant evolution provided by the Durian Theory.

References

- ANON. 1904. *Lobelia nicotianaefolia*. *Gdner's Chron.* III, 35: 194, 195.
- ANTHONY, J. 1936. A remarkable alpine *Lobelia* from Bhutan. *Notes R. bot. Gdn Edinb.* 19: 175–176.
- ARBER, A. 1928. The tree habit in Angiosperms: its origin and meaning. *New Phytol.* 27: 69–84.
- BEKETOFF, A. 1858. Ueber die morphologischen Verhältnisse der Blatt-theile zu einander und zum Stengel. *Linnaea* 29: 417–462.
- BENTHAM, G. 1873. Notes on the classification, history and geographical distribution of the Compositae. *J. Linn. Soc. (Bot.)* 13: 335–577.
- BRAMWELL, D. 1972a. A revision of the genus *Echium* in Macaronesia. *Lagascalia* 2: 37–115.
- 1972b. Endemism in the flora of the Canary Is. In D. H. VALENTINE (Ed.), *Taxonomy, Phytogeography and Evolution*: 141–159. Academic Press, London.
- BRIGHTMORE, D. 1968. Biological Flora of the British Isles. *Lobelia urens* L. *J. Ecol.* 56: 612–620.
- BURTT, B. L. 1974. Patterns of structural change in the flowering plants. *Trans. bot. Soc. Edinb.* 42: 133–142.
- CARLQUIST, S. 1962. A theory of paedomorphosis in dicotyledonous woods. *Phytomorphology*. 12: 30–45.
- 1965. *Island Life*. Natural History Press, New York.
- COE, M. J. 1967. The ecology of the alpine zone of Mount Kenya. *Monog. Biol.* 17: 1–136.
- CORNER, E. J. H. 1949. The Durian Theory or the origin of the modern tree. *Ann. Bot.* 13: 367–414.
- 1953. The Durian Theory extended — I. *Phytomorphology* 3: 465–476.
- 1954a. The Durian Theory extended — II. The arillate fruit and the compound leaf. *Phytomorphology* 4: 152–165.
- 1954b. The Durian Theory extended — III. Pachycauly and megaspermy — Conclusion. *Phytomorphology* 4: 263–274.
- 1964. *The Life of Plants*. Weidenfeld & Nicholson, London.
- 1966. *The Natural History of Palms*. Weidenfeld & Nicholson, London.
- 1967a. On thinking big. *Phytomorphology* 17: 24–28.
- 1967b. *Ficus* in the Solomon Islands and its bearing on the post-Jurassic history of Melanesia. *Phil. Trans. R. Soc. B.* 253: 23–159.
- COTTON, A. D. 1944. The megaphytic habit in the tree Senecios and other genera. *Proc. Linn. Soc. Lond.* 156: 158–168.
- CROIZAT, L. 1962. *Space, Time and Form. The Biological Synthesis*. Caracas.
- DARWIN, C. 1859. *On the Origin of Species*. Murray, London.

- DAUBENMIRE, R. F. 1947. Plants and Environment. A textbook of Plant Autecology. Wiley, New York.
- DAVIS, E. L. 1961. Medullary bundles in the genus *Dahlia* and their possible origin. *Amer. J. Bot.* **48**: 108–113.
- DIELS, L. 1934. Die paramos der äquatorialen Hoch-Anden. *Sber. preuss. Akad. Wiss.* **1934**: 57–68.
- EXELL, A. W. 1956. Supplement to the Catalogue of the Vascular Plants of S. Tomé (with Principe and Annobon). British Museum, London.
- FOSBERG, F. R. 1944. El Páramo de Sumapaz, Colombia., *J. N. Y. bot. Gdn* **45**: 226–234.
- FRIES, R. E. & T. C. E. FRIES. 1922. Die Riesen-Lobelien Afrikas. *Svensk bot. Tidskr.* **16**: 383–416.
- GATSUK, L. E., T. G. DERSVIS-SOKOLOVA, I. V. IVANOVA & L. M. SHAFRANOVA. 1974. Puti perckhoda at Kustarnikovykh form k travianistym v nekotorykh taksonakh pokrytosemennykh. *Trudy mosk. Obshch. ispyt. Priro.* **561**: 16–36.
- GAWADI, A. G. & G. S. AVERY. 1950. Leaf abscission and the so-called “abscission layer”. *Amer. J. Bot.* **37**: 172–180.
- GILBERT-CARTER, H. 1947. A Guide to the University Botanic Garden. Cambridge Univ. Botanic Garden.
- GOOD, R. d'O. 1974. The Geography of the Flowering Plants. 4th Ed. Longmans, London.
- HALLÉ, F. & R. A. A. OLDEMAN. 1970. Essai sur l'Architecture et la Dynamique de Croissance des Arbres Tropicaux. Masson, Paris.
- HEDBERG, O. 1964. Features of afro-alpine plant ecology. *Acta phytogeogr. suec.* **49**: 1–144.
- . 1969. Evolution and speciation in a tropical high mountain flora. *Biol. J. Linn. Soc.* **1**: 135–148.
- HEILBORN, O. 1925. Contributions to the ecology of the Ecuadorian páramos with special reference to cushion plants and osmotic pressure. *Svensk bot. Tidskr.* **19**: 153–170.
- HERKLOTS, G. A. C. 1972. Vegetables in South-East Asia. Allen & Unwin, London.
- HOFFMANN, O. 1892. Compositae. In A. ENGLER & K. PRANTL, Die Natürlichen Pflanzenfamilien IV, **5**: 187–391, Engelmann, Leipzig.
- HUMBERT, H. 1935. Sur un *Senecio* arborescent nouveau des hautes montagnes du Congo belge et sur les liens phylogénétiques des espèces alliées. *Bull. Soc. bot. Fr.* **81**: 830–848.
- . 1962. Flore de Madagascar et des Comores. 189^e famille Composées, Tome II. Mus. Nat. Hist. Nat., Paris.
- HUTCHINSON, J. 1946. A Botanist in Southern Africa. Gawthorn, London.
- JOHNSTON, H. H. 1886. The Kilima-Njaro Expedition., Kegan Paul, London.
- KNIGHT, T. A. 1795. Observations on the grafting of trees. *Phil. Trans. R. Soc.* **85**: 290–295.

- KOECHLIN, J. 1969. Contribution à l'étude morphologique du genre *Pachypodium*. *Adansonia* N. S. **9**: 403–420.
- LECOMTE, H. 1922. Les Bois de la Forêt de l'Analmazaotra. Paris.
- MABBERLEY, D. J. 1973a. Evolution in the Giant Groundsels. *Kew Bull.* **28**: 61–96.
- 1973b. 'Mutomboro' and 'Shukuku Gomen': *Senecio mannii* and *Senecio gigas*. In: The pachycaul species of *Senecio* and *Lobelia* in Africa: 15–28. Ph.D. thesis, Univ. of Cambridge.
- 1974a. Branching in pachycaul *Senecios*: the Durian Theory and the evolution of angiospermous trees and herbs. *New Phytol.* **73**: 967–975.
- 1974b. Pachycauly, vessel-elements, islands and the evolution of arborescence in 'herbaceous' families. *New Phytol.* **73**: 977–984.
- 1974c. The pachycaul *Lobelias* of Africa and St. Helena. *Kew Bull.* **29**: 535–584.
- 1975a. The Giant *Lobelias*; pachycauly, biogeography, ornithophily and continental drift. *New Phytol.* **74**: 365–374.
- 1975b. The pachycaul *Senecio* species of St. Helena, 'Cacalia materna' and 'Cacalia paterna'. *Kew Bull.* **30**: 413–420.
- MCDOUALL, K. 1927. The gardens at Logan. *J. R. hort. Soc.* **52**: 1–14.
- MELVILLE, R. 1953. Growth and plant systematics. *Proc. Linn. Soc. Lond.* **165**: 173–181.
- MENNINGER, E. A. 1967. *Fantastic Trees*. Viking, New York.
- METCALFE, C. R. & L. CHALK. 1950. *Anatomy of the Dicotyledons*. 2 vols. Oxford University Press.
- MEUSEL, H. 1952. Über Wuchsformen, Verbreitung und Phylogenie einiger mediterran-mitteuropäischer Angiospermen-Gattungen. *Flora (Jena)* **139**: 333–393.
- PONTECORVO, G. 1972. Alpine plants of the Callejón de Huálas. In -R. C. ELLIOTT (Ed.), 4th International Rock Garden Plant Conference 1971: 51–97. Alpine Garden Soc., London.
- Von RÜPPELL, E. 1836. Bemerkungen über Abyssinien, im Bezug auf der Physiognomie der Landschaft (Forsetzung). *Zeitsch. Phönix Frankfurt-am-Main* **120**: 479–480.
- 1840. *Reise in Abyssinia, Abbildung*. Frankfurt.
- SALT, G. 1954. A contribution to the ecology of upper Kilimanjaro. *J. Ecol.* **42**: 375–423.
- SCHAFFALITZKY De MUCKADELL, M. 1959. Investigations on aging of apical meristems in woody plants and its importance in silviculture. *Forst. ForsVaes. Danm.* **25**: 310–455.
- SCOTT, H. 1935. Coleoptera associated with the giant *Lobelias* and arborescent *Senecios* of Eastern Africa. *J. Linn. Soc. (Zool.)* **39**: 235–284.
- 1940. General and zoogeographical considerations regarding the Coleoptera associated with giant *Lobelias* and *Senecios* in Eastern Africa. *Int. Congr. Ent.* **6**, **2**: 443–446.

- . 1958. Biogeographical research in High Simien (Northern Ethiopia) 1952-3. *Proc. Linn. Soc. Lond.* **170**: 1-91.
- SHREVE, F. 1914. The direct effects of rainfall on hygrophilous vegetation. *J. Ecol.* **2**: 82-98.
- SMITH, A. C. & M. F. KOCH. 1935. The genus *Espeletia*: a study in phylogenetic taxonomy. *Brittonia* **1**: 479-530.
- SMITH, D. L. 1967. The experimental control of inflorescence development in *Carex*. *Ann. Bot.* **31**: 19-30.
- STEBBINS, G. L. 1951. Natural selection and the differentiation of Angiosperm families. *Evolution* **5**: 299-324.
- Van STEENIS, C. G. G. J. 1958. Rejuvenation as a factor for judging the status of vegetation types: the Biological Nomad Theory. *Proc. Kandy Symp. U.N.E.S.C.O.* : 212-218.
- TENOPYR, L. A. 1918. On the constancy of cell-shape in leaves of varying shape. *Bull. Torrey bot. Club* **45**: 51-76.
- TROLL, C. 1947. Der asymmetrische Aufbau der Vegetationszonen und Vegetationsstufen auf der Nord und Südhalbkugel. *Ber. geobot. ForschInst. Rübel* **1947**: 46-83.
- TUYAMA, T. 1936. *Plantae Boninenses novae vel criticae V.* *Bot. Mag. (Tokyo)* **50**: 129-134.
- UITTEN, H. 1928. Ueber den Zusammenhang zwischen Blattnervatur und Sprossverzweigung. *Recl. Trav. bot. néerl.* **25**: 390-483.
- VASSAL, J. 1970. Contribution à l'étude de la morphologie des plantules d'*Acacia*. *Acacias insulaires des océans indien et pacifique: Australie, Formose, Iles Maurice et Hawaii.* (*Trav. Lab. For. Toul.* I, **9**: art. VIII) *Bull. Soc. Hist. nat. Toulouse* **106**: 191-276.
- WARDLE, P. 1971. An explanation for alpine timberlines. *N.Z. J. Bot.* **9**: 371-402.
- WHITE, F. 1971. The taxonomic and ecological basis of chorology. *Mitt. bot. StSamml., Münch.* **10**: 91-112.
- WILLIS, J. C. 1973. *A Dictionary of the Flowering Plants and Ferns*. 8th ed. Revised by H. K. AIRY SHAW. Cambridge University Press.
- WIMMER, F. E. 1956. Campanulaceae-Lobelioideae. I teil. In A. ENGLER & L. DIELS, *Das Pflanzenreich, Regni Vegetabilis Conspectus IV*, **276a**: 1-260. (reprint of 1943 ed.). Akad. Verlag, Berlin.
- . 1968. Supplementum. *Idem*, **276c**: 815-916.
- WOOD, D. 1971. The adaptive significance of wide altitudinal range for montane species. *Trans. bot. Soc. Edinb.* **41**: 119-124.
- WOODHEAD, N. 1951a. Biological Flora of the British Isles. *Lobelia* L. *J. Ecol.* **39**: 456-457.
- . 1951b. *Idem*, *Lobelia dortmanna* L. *J. Ecol.* **39**: 458-464.
- ZIMMERMANN, M. H. & P. B. TOMLINSON. 1972. The vascular system of Monocotyledonous stems. *Bot. Gaz.* **133**: 141-155.